

## STAGE AND SIZE STRUCTURE OF THREE SPECIES OF OAKS IN CENTRAL COASTAL CALIFORNIA

IAN S. PEARSE

Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850 and  
Illinois Natural History Survey, 1816 S Oak St, Champaign, IL 61820  
ianspearse@gmail.com

SOPHIE GRISWOLD AND DESIRREE PIZARRO

Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850

WALTER D. KOENIG

Cornell Lab of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850 and  
Department of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853

### ABSTRACT

Oaks are foundational species in much of California, and many oak populations in the state may be in jeopardy due to a lack of recruitment of young trees. Despite considerable interest in this problem, there have been few comprehensive surveys of all stages of oak development. We surveyed all stages of three oaks: *Quercus lobata*, *Q. douglasii*, and *Q. agrifolia* in a forest plot with mixed land-use in central coastal California. We found abundant seedlings of all oak species, but an apparent paucity of *Q. lobata* and *Q. douglasii* saplings. First year seedlings of all species were less abundant in parts of the study site with cattle grazing, but later-stage seedlings of *Q. lobata* and *Q. douglasii* were equally abundant across land-use types. *Quercus agrifolia* seedlings were associated with non-grazed areas; *Quercus agrifolia* late-stage seedlings in the grazed area were smaller and less abundant than in non-grazed areas. *Quercus agrifolia* seedlings of all stages tended to be clustered around conspecific mature trees. *Quercus lobata* late-stage seedlings, and to a lesser degree those of *Q. douglasii*, were often distant from any potential parent tree. These data indicate that young stages of the three species of oak have different spatial distributions and occur in different abundances at two sites with different grazing regimes. They are also consistent with a relative lack of regeneration in *Q. lobata* and *Q. douglasii*, although it remains to be determined that the small number of saplings of these species observed is insufficient to replace mortality of mature trees. This survey provides a baseline from which future resampling can assess the long-term demographic success of three Californian oak species.

Key Words: regeneration, demography, *Quercus*.

Californian oaks are a dominant component of at least a third of the forest and savanna ecosystems of the state (Pavlik et al. 1991). However, there has been recent concern for oak populations, as there is a perceived lack of regeneration of oak forests and a lack of young tree stages (Griffin 1976; Tyler et al. 2006). Studies have attributed the lack of oak regeneration to various causal factors (Griffin 1971; Borchert et al. 1989; Callaway and Davis 1998; Gordon and Rice 2000), while others have questioned the severity of regeneration problem altogether (Tyler et al. 2006).

The apparent lack of recruitment of two common California oaks, *Quercus lobata* Née and *Q. douglasii* Hook. & Arn. (Fagaceae), have prompted numerous causal explanations for seedling mortality and lack of regeneration in these species, including cattle grazing (Hall et al. 1992; Tyler et al. 2008; Reiner and Craig 2011), competition from non-native grasses (Griffin 1971; Gordon and Rice 2000), altered herbivore populations (Griffin 1971; Borchert et al. 1989;

Callaway and Davis 1998; Davis et al. 2011), and increased drought stress (Mahall et al. 2009). Each of these factors has undergone widespread anthropogenic change in the last two centuries, thus potentially explaining the apparently poor recruitment currently suffered by oak populations (reviewed by Tyler et al. 2006). However, the relative importance of each of these factors may be site specific. For example, while grazing may decrease seedling abundance at some sites (Reiner and Craig 2011), even sites without livestock grazing may experience a lack of seedling recruitment (Griffin 1971). The lack of a single causal factor in altering oak populations calls for a more integrative approach in assessing oak population dynamics.

A recent conceptual review (Tyler et al. 2006) and meta-analysis (Zavaleta et al. 2007) of California oak recruitment both suggested that two Californian oaks, valley oak (*Q. lobata*) and blue oak (*Q. douglasii*), suffer from declining populations. Both studies concluded that site-specific causes may affect recruitment of these

species. Moreover, they indicated that detailed demographic models are needed to address the question of whether low observed recruitment levels are actually insufficient to replace stands of long-lived adults. Likewise, a detailed demographic analysis of oak populations could ask specifically which life stages most limit population growth (Tyler et al. 2006; Zavaleta et al. 2007; Davis et al. 2011). Meanwhile, studies have suggested that a third species of Californian oak, *Q. agrifolia* Née, may not be undergoing similar low regeneration rates as its two sympatric congeners, even though it may be affected by some of the same recruitment challenges (Callaway and Davis 1998; Mahall et al. 2009).

While studies have successfully documented multiple site specific factors likely affecting populations of Californian oaks, there is still a relative lack of the explicit demographic modeling of oak populations needed to quantify the risk to oak populations and to assess which life stages of oaks are of the highest conservation value. The only current study that explicitly reconstructs *Q. lobata* demography uses an experimental approach, which is very valuable in determining causal factors that limit *Q. lobata* success (Davis et al. 2011). Observational studies that thoroughly survey oak populations that are both geographically referenced and include all life stages of the oaks complement experimental studies. Such surveys will be valuable because they can be easily resampled in order to directly assess vital rates and stage transitions. At the same time, comprehensive site surveys observe oak populations across all microhabitats at a site, which is difficult in manipulative studies.

Here we present a baseline survey of the oaks on a portion of Hastings Natural History Reserve (HNHR) and the adjacent Oak Ridge Ranch (ORR) property in Monterey County of central coastal California. We surveyed the size, stage, and geographic location of 19,755 individuals of the three dominant oak species (*Q. lobata*, *Q. douglasii*, and *Q. agrifolia*) in a 52.6 hectare area encompassing forest, grassland, and savannah habitats. This survey also encompassed areas with strikingly different recent land use histories, as HNHR has been protected from cattle grazing since 1937, but ORR continues to experience significant regular cattle grazing. We use this survey primarily to establish a baseline for parameterizing future demographic models of oak populations, and we make this baseline data available to the general scientific community. We analyzed the size structure and spatial distribution of early and late seedling stages of these oaks in order to ask to what degree habitat type and land use affect the size of late-stage seedlings and the proximity of seedlings to a potential parent.

## METHODS

### Study Area and Natural History

The survey was conducted on Haystack Hill and surrounding areas (36.385114 N, -121.561906 W) on Hastings Natural History Reservation (HNHR) and the adjacent Oak Ridge Ranch (ORR) (Fig. 1). The study area is typical of coast range oak habitat, is the site of several studies of oak populations (White 1966; Griffin 1971, 1976; Koenig and Knops 2007), and is central (within 70 km of 1/3 of the study sites) to the sites used in a recent meta-analysis of Californian oak populations (Zavaleta et al. 2007). The study area has a Mediterranean climate typical of California's coast range. In the year of the survey, the average rainfall was 475 mm, which was slightly less than the 30 year average for the site (540 mm – Hastings Weather Station <http://www.hastingsreserve.org/weather/Weather.html>). The study area was roughly delimited by the contour of the hill. We excluded a large patch of dense chaparral that would have been within the study, as the area was too densely vegetated to use the same survey techniques as in other areas and contained few oak trees, with the exception of a small number of *Q. agrifolia* individuals at the bottom of dry washes that descended the hillside through chaparral.

The study area was divided into three habitat types based on tree cover and groundcover type: forest, savanna, and grassland (Griffin 1990). 'Forest' had a complete canopy cover. Forest understory was dominated by poison oak (*Toxicodendron diversilobum* [Torr. & A. Gray] Greene) and had little to no grass cover. One forest region had a substantial stand of madrone (*Arbutus menziesii* Pursh), whereas oaks dominated all others. 'Savanna' had a partial canopy cover and an understory of native and non-native grasses including *Avena* L. sp., *Bromus hordeaceus* L., *B. diandrus* Roth, *Hordeum* L. sp., *Stipa pulchra* Hitchc., and *Aira caryophyllea* L., as well as forbs such as *Madia gracilis* (Sm.) D. D. Keck, *Asclepias eriocarpa* Benth., *Plagiobothrys* Fisch. & C.A. Mey. sp., and *Amsinckia menziesii* (Lehm.) A. Nelson & J.F. Macbr. 'Grasslands' had sparse to no tree cover and were dominated by the same mix of grasses and forbs. Small remnants of perennial grasslands (sensu Griffin 1990) dominated by *Stipa pulchra* were included in this category. There was considerable variation in both slope and aspect of habitat types within the study area, but both study sites (HNHR and ORR) had both steep and relatively flat forests, grasslands, and savannahs. One difference between the two sites was the presence of a small creek bed at the HNHR site that had a high abundance of *Q. agrifolia* seedlings.

The study site was divided approximately down the middle by a fence separating HNHR



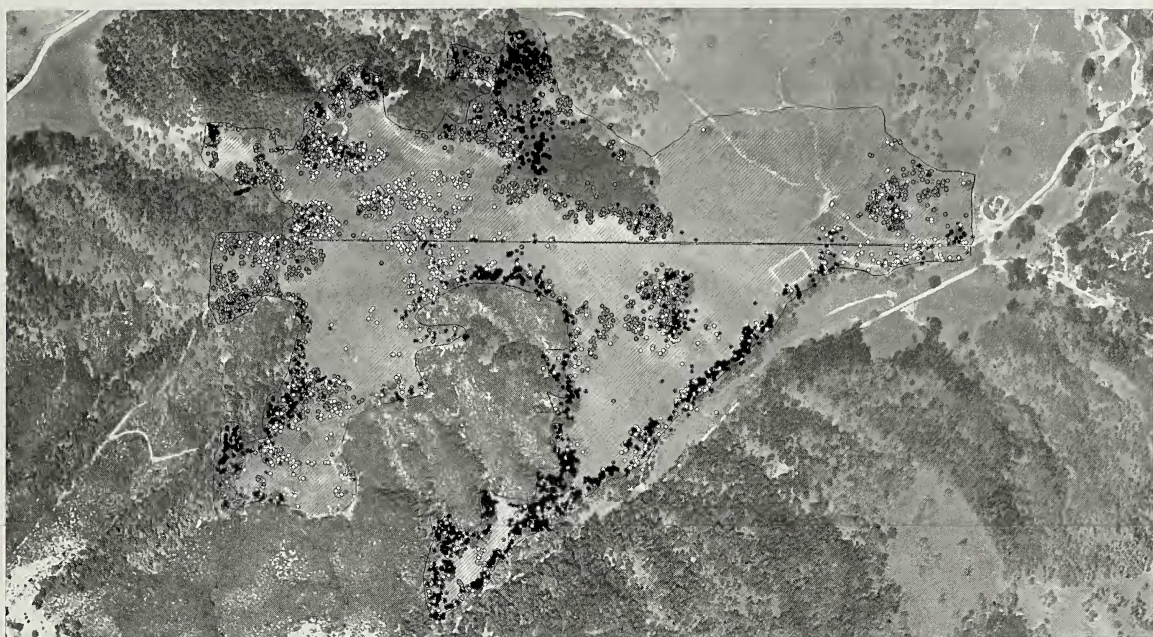


FIG. 1. A map of the survey area (highlighted in light dashes and outlined with a dotted line). The survey is divided roughly in half by a property line (central E-W line), where the northern property (Oak Ridge Ranch) is grazed and the southern property (Hastings Natural History Reserve (HNHR)) is ungrazed. In May–June 2012, we surveyed and recorded the location of all valley oak (*Q. lobata*, white dots), blue oak (*Q. douglasii*, grey dots), and coast live oak (*Q. agrifolia*, black dots) first year seedlings, late-stage seedlings, saplings, and trees within the demarcated study area.

from ORR. The land use of the two areas can be summarized as follows. Prior to 1930, both sites had a history of mixed land use including ranching, timber harvest, and small-scale agriculture (Griffin 1990). HNHR was donated to the University of California in 1937 at which point all grazing and agriculture was stopped. At ORR, moderate year-round cattle grazing continues to present day, including during the active survey period, although no tillage or significant timber harvest has been recorded within the study area within recent history. While oak plantings and restoration efforts have been made in other portions of HNHR, none of these activities have occurred within the study area.

The year preceding our survey had a moderate to good acorn crop for all three oak species. Based on the Koenig visual count method (Koenig et al. 1994a), the 2011 *Q. lobata* acorn crop was 15% greater than the 30-year mean *Q. lobata* crop (Pearse et al. 2014). Likewise, the 2011 *Q. douglasii* acorn crop was 63% greater than its 30-year mean, and the 2011 *Q. agrifolia* acorn crop was 29% greater than its 30-year mean.

### Survey Methods

We surveyed all valley oak, blue oak, and coast live oak individuals within the study area in May through early July 2012. We marked 10 m wide

transects across the study area and used a GPS to record the locality of each oak within the area to an accuracy of 5 m. For each individual, we recorded one of four growth stages. Seedlings were first year germinants from acorns. All had unbranched stems, and most were still connected to a partially buried acorn. Late-stage seedlings were over one year old, less than 1.5 meters in height, had branched or multiple stems, and lacked a connected acorn. Saplings were greater than 1.5 meters in height, less than 10 cm DBH, and had not yet begun to produce fruit or flowers. Adult trees were over 10 cm DBH. We considered these classes to be biologically useful, as demographic parameters including growth rate, survivorship, and reproduction likely vary between stages (e.g., Griffin 1971; Koenig and Knops 2007). For all late-stage seedlings, we also recorded height and canopy width and calculated seedling volume as height  $\times$  width<sup>2</sup>. For all first-year seedlings, late-stage seedlings, and saplings, we also calculated Euclidean distance to the nearest conspecific adult tree. We tagged each adult tree and recorded which first year seedlings, late-stage seedlings, and saplings were within 20 m of its trunk.

### Statistical Analysis

While the two landscape level factors – habitat and property, the latter corresponding to differ-



TABLE 1. THE DENSITY OF THREE OAK (*QUERCUS*) SPECIES (TREES/HECTARE) IN THREE HABITAT TYPES SPANNING THE UNGRAZED HASTINGS NATURAL HISTORY PRESERVE (HNHR) AND GRAZED OAK RIDGE RANCH (ORR). All trees (>10 cm DBH), saplings (>1.5 m tall), late-stage seedlings (multiple stems, no attached acorn), and first-year seedlings (single stem, often acorn still attached) within the total 52.57 ha survey area were recorded resulting in 19,755 records of oak individuals.

		Forest		Savannah		Grassland	
		HNHR	ORR	HNHR	ORR	HNHR	ORR
<i>Quercus lobata</i>	Area (ha)	8.21	8.89	8.23	7.73	10.83	8.65
	1st year seedling	161.75	7.2	49.09	5.3	16.34	0.55
	Late stage seedling	47.14	17.55	24.79	54.59	15.51	18.47
	Sapling	0.24	0	0	0	0.09	0.09
	Tree	17.54	10.01	13.49	6.47	2.4	0.37
<i>Quercus douglasii</i>	1st year seedling	18.39	176.04	84.93	34.67	3.23	0.09
	Late stage seedling	29.6	194.94	94.9	60.28	5.26	2.4
	Sapling	0.49	0	0	0	0.09	0
	Tree	11.33	69.74	22.72	6.21	0.09	0.83
<i>Quercus agrifolia</i>	1st year seedling	455.18	23.17	57.84	1.29	61.68	0.28
	Late stage seedling	209.38	76.83	24.18	8.8	6.74	3.42
	Sapling	15.23	0.45	0	0	0.55	0
	Tree	55.05	27.67	6.44	0.91	0.92	0

ent land use – are spatially non-independent, we used these data to build a case study of oak populations at a single, large site. Specifically, our goal was to explore variation in 1) the size of late-stage seedling oaks, as this size class may escape grazing at large sizes (either by being tall or very wide), 2) the distance of seedlings and late-stage seedling oaks from a potential (conspecific) parent tree, and 3) the composition of oak seedlings in the understory of individual adult trees. All statistics were calculated in R using package *car* (R Core Development Team 2008; Fox and Weisberg 2011). Our georeferenced dataset is made available at the Dryad data depository <http://dx.doi.org/10.5061/dryad.467g5> and on the authors' websites <http://www.nbb.cornell.edu/wkoenig>; <http://ianpearse.wordpress.com>.

RESULTS

Habitat and Land-use Associations

We surveyed 52.6 ha and gathered data on a total 19,755 individuals of the three oak species across both properties (HNHR and ORR) and all habitats (Fig. 1, Table 1). The surveyed area of each habitat type at each property was similar, and we report the densities of oaks at each stage in each habitat type on the two properties (Table 1). *Quercus lobata* seedlings were more abundant at HNHR, the ungrazed site, than at ORR, the grazed site – 1909 seedlings versus 111 (Table 1). However, this difference did not carry into the late-stage seedling individuals, and there were slightly fewer late-stage seedling *Q. lobata* at HNHR than at ORR (759 versus 778). At HNHR both *Q. lobata* seedlings and late-stage seedling stages tended to be located in forested habitats, whereas at ORR, they were associated

with savannah, although the distribution of overstory trees only partially reflected this trend. All growth stages of *Q. douglasii* were uncommon in grasslands at all sites (Table 1). There was a greater abundance of early growth stages of *Q. douglasii* at ORR than at HNHR (4059 versus 1966), reflecting the distribution of adult trees at the two sites (677 versus 281). There was a full-canopied *Q. douglasii* forest on ORR, and all growth stages of *Q. douglasii* at ORR were more closely associated with forest than at HNHR, where *Q. douglasii* was more abundant in open savannah habitat. *Quercus agrifolia* was associated with full-canopied forest habitats at both sites and was particularly abundant in HNHR forests. *Quercus agrifolia* was also more abundant in HNHR grasslands and savannas than the same habitat types at ORR. There were strikingly fewer *Q. agrifolia* first year seedlings in all habitats on ORR than on HNHR (219 versus 4881), which would be consistent with an impact of grazing on *Q. agrifolia* seedling abundance. For *Q. agrifolia*, this trend persisted into late-stage seedlings, where there were fewer *Q. agrifolia* late-stage seedlings at ORR than at HNHR (788 versus 1991). There were few saplings of both *Q. lobata* and *Q. douglasii* in all habitats at both properties (four *Q. lobata* saplings and five *Q. douglasii* seedlings), consistent with perceived recruitment problems with these species. In contrast, *Q. agrifolia* saplings were reasonably common (n = 135), almost all of which were associated with forest sites on the ungrazed HNHR property (Table 1).

Size of Late Stage Seedlings

We measured the volume of late-stage seedlings (excluding first-year seedlings) (Fig. 2).



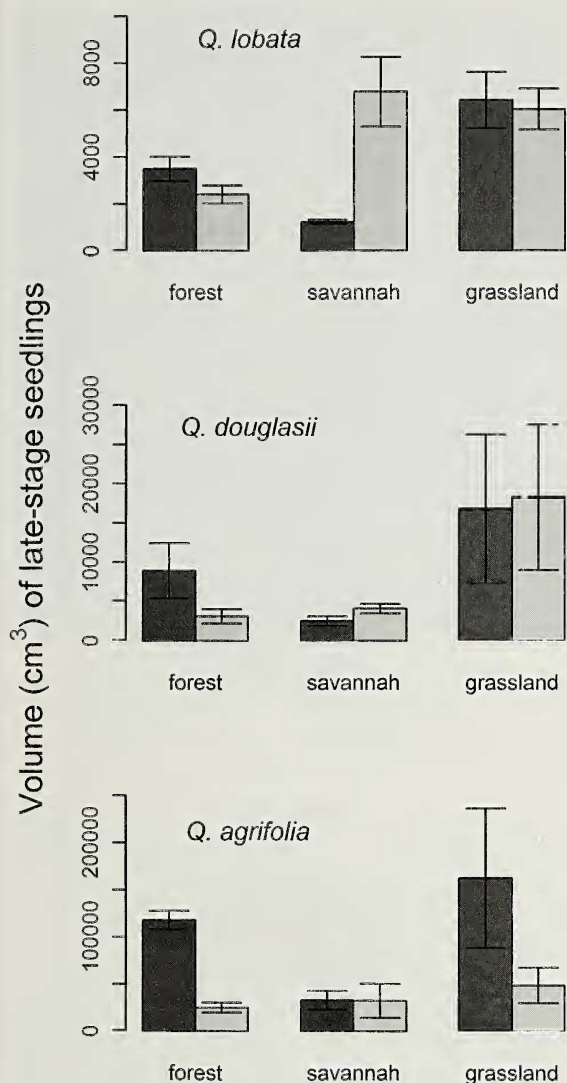


FIG. 2. The volume of late-stage seedlings of *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* in three habitat types on ungrazed (HNHR, dark grey) and grazed (ORR, light grey) properties. Our designation of "late-stage seedling" included oaks that were less than 1.5 m in height, had multiple stems, and no attached acorn. This size of this stage may be particularly important to oak regeneration, as late-stage seedlings persist over many years and are susceptible to grazing, especially when small. Bars are means  $\pm$  SE.

*Quercus lobata* late-stage seedlings tended to be larger in more open habitats such as grasslands irrespective of whether the site was grazed or not (Fig. 2). *Quercus lobata* seedlings in savannahs were four times larger on ORR than on HNHR (Fig. 2) and similar in size in other habitat types, a finding that is not consistent with cattle grazing being a factor limiting seedling growth of this species.

*Quercus douglasii* late-stage seedlings showed similar size trends to *Q. lobata*, with larger late-

stage seedlings in grasslands than in other habitat types (Fig. 2). Unlike *Q. lobata*, they were roughly the same size across land-use types in all habitats.

*Quercus agrifolia* late-stage seedlings showed the strongest size association with land use type of the three species. In both grasslands and forests, *Q. agrifolia* late-stage seedlings at HNHR were 300–400% larger than those in the same habitats on ORR (Fig. 2). *Quercus agrifolia* late-stage seedlings in savannah habitat were smaller than in other habitats (Fig. 2). The variation in size of seedlings was greatest in grassland habitats.

### Spatial Distribution of Seedlings

We measured the distance from each first year seedling and late stage seedling to its nearest mature conspecific tree (i.e., potential parent) (Fig. 3). *Quercus lobata* first-year seedlings averaged 12.4 meters from the nearest potential parent. *Quercus lobata* late stage seedlings were on average further from the nearest potential parent than seedlings of the other species, and this distance was even greater on ORR than on HNHR (15.6 m and 14.3 m respectively, Fig. 3). *Quercus douglasii* seedlings were generally closer to a potential parent than *Q. lobata* seedlings, likely reflecting the density of stands of these tree species (Fig. 3). Both *Q. douglasii* first-year and late-stage seedlings averaged eight m from the nearest potential parent on HNHR (Fig. 3). On ORR, first-year *Q. douglasii* seedlings averaged 4.7 m from the nearest potential parent and late-stage seedlings averaged seven m. *Quercus agrifolia* seedlings averaged 7.5 m from the nearest potential parent, a value that did not vary by either seedlings class ( $F_{1,3855} = 2.0$ ,  $P = 0.16$ ) or property ( $F_{1,3855} = 0.002$ ,  $P = 0.96$ , Fig. 3).

We also measured the composition of the seedling oak community underneath mature trees of each of the three oak species and found that the understories of both *Q. douglasii* and *Q. agrifolia* were dominated by their conspecific seedlings (Fig. 4). In contrast, the understories of *Q. lobata* trees had a roughly even distribution of seedlings from all three oak species. Similarly, *Q. lobata* seedlings were the least abundant component of the understories of either *Q. douglasii* or *Q. agrifolia*.

### DISCUSSION

The size and age distributions of the three species of oaks surveyed in this study varied between properties with different land-use history, but these differences were fairly subtle. There were fewer valley oak (*Q. lobata*) first-year seedlings per adult tree on the grazed site (ORR) than on the ungrazed site (HNHR).



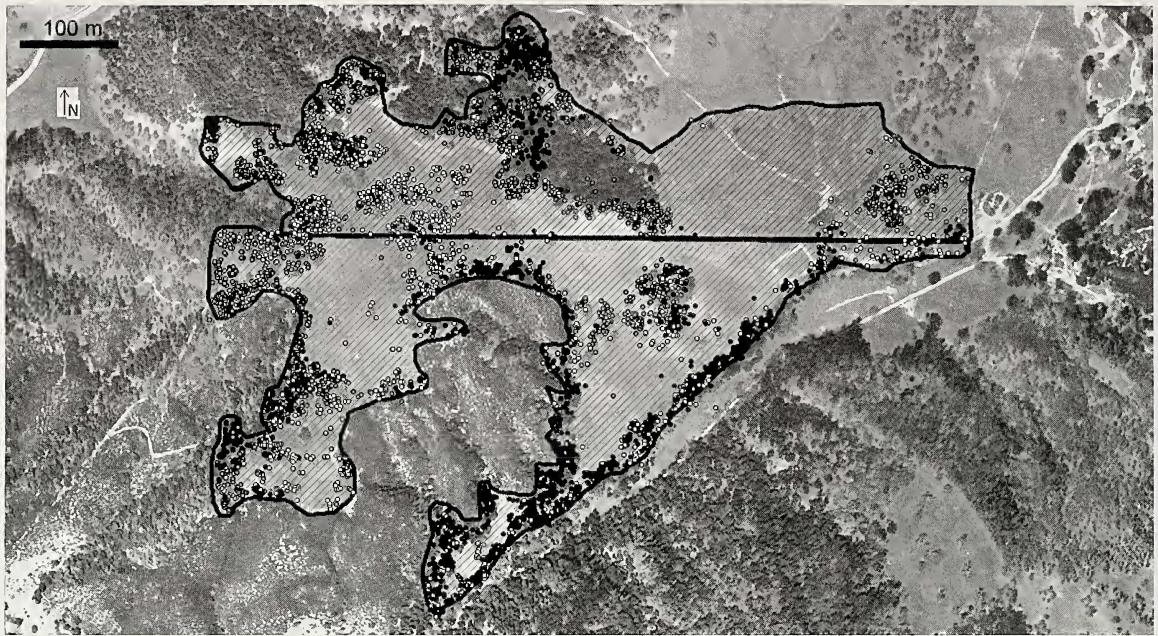


FIG. 3. The distribution of the distance of *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* first year seedlings (dashed line) and late-stage seedlings (solid line) to their nearest conspecific (i.e., potential parent) tree at the ungrazed site (HNHR) and grazed site (Oak Ridge Ranch). Valley oak late-stage seedlings and to a lesser degree first year seedlings are located at a greater distance from a potential parent than the other two species.

However, the abundance of late-stage seedlings was similar at both sites (Table 1). Moreover, *Q. lobata* late-stage seedlings were on average larger at the grazed site, further suggesting that cattle grazing may affect the survival of first-year seedlings, but may have little or no effect on the long-term survival of established seedlings. *Quercus douglasii* populations had generally the same associations as *Q. lobata* with the two major land use patterns (Table 1, Fig. 2), except that there was a large number of first-year and late-stage *Q. douglasii* seedlings in a dense forest patch on ORR (Table 1). The larger size of late-stage seedlings at the grazed site suggests that cattle grazing does not limit (and may even promote) the growth of these seedlings at our study area.

The land-use differences in this survey are consistent with effects of cattle grazing on *Q. douglasii* and *Q. lobata* observed in other studies. For example, experimental manipulation of grazing did not affect the survivorship of late-stage (2-year old) seedlings in a Sierra Nevada foothills population of *Q. douglasii*. (Hall et al. 1992), and grazing decreased the total abundance of naturally recruiting *Q. douglasii* seedlings (likely including a large portion of first-year seedlings) in only one out of four years (Reiner and Craig 2011). Livestock grazing may still be a significant mortality factor for *Q. lobata* and *Q. douglasii*; however, our results suggest that other mortality factors are potentially more important even in ungrazed sites.

Interestingly, our survey found fewer (Table 1) and smaller (Fig. 2) early-stage *Q. agrifolia* individuals on the grazed property (ORR) than on the ungrazed property (HNHR). Unlike in *Q. douglasii*, *Q. agrifolia* later-stage seedlings were both smaller and less abundant (with reference to mature trees) on ORR than on HNHR (Fig. 2, Table 1). Moreover, there were far more *Q. agrifolia* saplings per mature tree on HNHR than on ORR (Table 1). As non-adult stages appear to be more represented at HNHR than at ORR, this suggests that *Q. agrifolia* population growth on HNHR may be higher than on the grazed adjacent property. *Quercus agrifolia* populations are thought to be stable or even increasing in many regions with high forest or shrub cover, but are unable to colonize open habitat, presumably because shrubs provide a refuge from wildlife or livestock grazing (Callaway and Davis 1998). In the current survey, *Q. agrifolia* was strongly associated with habitats with greater shrub and tree cover, and livestock grazing may have imposed a sufficient herbivore pressure to partially negate the protective effect of high vegetation cover for *Q. agrifolia* seedlings.

The seedlings of each of the three oak species had unique spatial distributions with reference to their potential parental trees. The distribution of first-year seedlings likely reflects patterns of acorn fall and immediate dispersal. As acorn production is pulsed (i.e., varies dramatically from year to year) and synchronous between trees



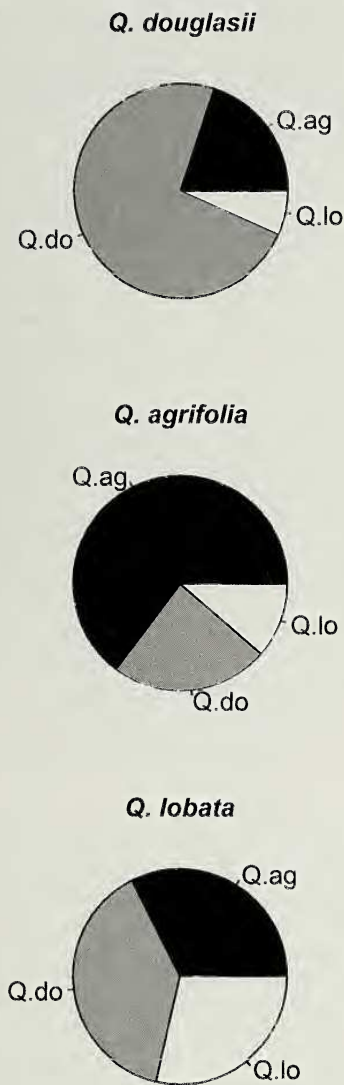


FIG. 4. The species identity of all immature oaks (first year and late-stage seedlings) within 20 m of a valley oak (*Q. lobata* = *Q. lo*), blue oak (*Q. douglasii* = *Q. do*), and coast live oak (*Q. agrifolia* = *Q. ag*). The understories of both blue oak and live oak were dominated by conspecifics (likely acorn fall from the focal tree), however the understory of valley oak had a roughly even representation of all three species.

(Koenig et al. 1994b), the distribution of first-year seedlings may vary substantially from year to year. On the other hand, the late-stage seedlings of oaks in this habitat may be very long-lived (Koenig and Knops 2007), so their distribution is unlikely affected by temporal variation in acorn crop. *Quercus lobata* first year seedlings were clustered around potential parental trees, likely reflecting patterns of acorn fall. Late-stage *Q. lobata* seedlings, however, were on average further from a potential parent, especially on the grazed property (Fig. 3). This, in combination with few seedlings altogether at

some sites, resulted in an underrepresentation of *Q. lobata* seedlings in the understory of *Q. lobata* mature trees (Fig. 4). *Quercus douglasii* seedlings were more abundant under their parent tree (Fig. 4), although late-stage seedlings tended to be located further from a potential parent than first-year seedlings (Fig. 3). Both first year and late-stage *Q. agrifolia* seedlings were strongly clustered around potential parental trees (Fig. 3), and *Q. agrifolia* seedlings were highly represented in the understories of *Q. agrifolia* trees (Fig. 4).

These results suggest a hierarchy in the ability of oak seedlings to colonize open habitat. *Quercus lobata* was often found far from its parental species, consistent with previous studies showing that *Q. lobata* seedlings better tolerate dry habitats (Mahall et al. 2009) and deer browsing (Tyler et al. 2008) better than *Q. agrifolia*. *Quercus douglasii* has been shown to tolerate dry, exposed habitats (Griffin 1971), but it may be negatively affected by direct competition from non-native grasses in open areas (Gordon and Rice 2000) and is associated with shrub cover (Callaway 1992). *Quercus agrifolia* has been shown to be strongly associated with shrubby or forested habitat, which provides protection from herbivores (Callaway and Davis 1998).

The factors that limit oak populations are thought to be somewhat site-specific. This has led to both studies that attempt to find those factors that are important across many site (Zavaleta et al. 2007) and detailed studies that attempt to assess the causal factors limiting oak seedling success at individual sites (Davis et al. 2011). Our study will be useful in both of these goals. By establishing a baseline survey at a site, where the history of factors that could potentially affect oak populations (e.g., grazing, habitat affiliation, wildlife density) is well documented, our study can easily be combined with other surveys at different geographic locations in order to assess the generality of these factors. Likewise, by having a population of oaks where all stages are surveyed and georeferenced, this survey opens the possibility of resampling to determine the key demographic limitations at this representative site.

Explicit demographic models of Californian oak populations are important to understand the sustainability of the state's oak populations (Davis 2011). This study provides a thorough baseline estimate of populations of *Q. lobata*, *Q. douglasii*, and *Q. agrifolia* that can be used by future resampling and modeling efforts to estimate demographic transitions between life-history stages and thus the long-term dynamics of oak populations. For example, at the same site, a marked population of blue oak late-stage seedlings has persisted with little growth, little mortality, and no transitions to saplings within

the past 60 years (Koenig and Knops 2007). Moreover, there are currently no robust estimates of age-biased mortality for adult valley oaks, which is a critical parameter in estimating the necessary rate of replacement by seedlings (Tyler et al. 2006). By marking a large number of trees and seedlings, as well as the few observed saplings, resampling of this study may observe enough stage-transitions to accurately parameterize demographic models of oak populations at a large, natural site.

#### ACKNOWLEDGMENTS

We thank Vince Voegeli and the management of Oak Ridge Ranch for access to the study site. This study was supported by an NSF REU grants DEB-1021417 and DEB-1212885 and NSF grant DEB 0816691 to WDK.

#### LITERATURE CITED

- BORCHERT, M. I., F. W. DAVIS, J. MICHAELSEN, AND L. D. OYLER. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. *Ecology* 70:389–404.
- CALLAWAY, R. M. 1992. Effect of shrubs on recruitment of *Quercus douglasii* and *Quercus lobata* in California. *Ecology* 73:2118–2128.
- AND F. W. DAVIS. 1998. Recruitment of *Quercus agrifolia* in central California: the importance of shrub-dominated patches. *Journal of Vegetation Science* 9:647–656.
- DAVIS, F. W., C. M. TYLER, AND B. E. MAHALL. 2011. Consumer control of oak demography in a Mediterranean-climate savanna. *Ecosphere* 2:108, doi:10.1890/ES11-00187.1
- FOX, J. AND S. WEISBERG. 2011. An R Companion to Applied Regression, Second Edition. Sage Publications, Thousand Oaks, CA.
- GORDON, D. R. AND K. J. RICE. 2000. Competitive suppression of *Quercus douglasii* (Fagaceae) seedling emergence and growth. *American Journal of Botany* 87:986–994.
- GRIFFIN, J. R. 1971. Oak regeneration in upper Carmel Valley, California. *Ecology* 52:862–868.
- . 1976. Regeneration in *Quercus lobata* savannas, Santa Lucia Mountains, California. *American Midland Naturalist* 95:422–435.
- . 1990. Flora of Hastings Reservation, Carmel Valley, California. Third Edition. Regents of the University of California, Berkeley, CA.
- HALL, L. M., M. R. GEORGE, D. D. MCCREARY, AND T. E. ADAMS. 1992. Effects of cattle grazing on blue oak seedling damage and survival. *Journal of Range Management* 45:503–506.
- KOENIG, W. D. AND J. M. H. KNOPS. 2007. Long-term growth and persistence of blue oak (*Quercus douglasii*) seedlings in a California oak savanna. *Madroño* 54:269–274.
- , W. J. CARMEN, M. T. STANBACK, AND R. L. MUMME. 1994a. Estimating acorn crops using visual surveys. *Canadian Journal of Forest Research (Revue Canadienne De Recherche Forestiere)* 24:2105–2112.
- , R. L. MUMME, W. J. CARMEN, AND M. T. STANBACK. 1994b. Acorn production by oaks in central coastal California: variation within and among years. *Ecology* 75:99–109.
- MAHALL, B. E., C. M. TYLER, E. S. COLE, AND C. MATA. 2009. A comparative study of oak (*Quercus*, Fagaceae) seedling physiology during summer drought in southern California. *American Journal of Botany* 96:751–761.
- PAVLIK, B. M., P. C. MUICK, S. G. JOHNSON, AND M. POPPER. 1991. Oaks of California. Cachuma Press and California Oak Foundation, Los Olivos, CA.
- PEARSE, I. S., W. D. KOENIG, AND J. M. H. KNOPS. 2014. Cues versus proximate drivers: testing the mechanism behind masting behavior. *Oikos* (in press).
- R DEVELOPMENT CORE TEAM. 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website <http://www.R-project.org/> (accessed Dec 2010).
- REINER, R. AND A. CRAIG. 2011. Conservation easements in California blue oak woodlands: testing the assumption of livestock grazing as a compatible use. *Natural Areas Journal* 31:408–413.
- TYLER, C. M., F. W. DAVIS, AND B. E. MAHALL. 2008. The relative importance of factors affecting age-specific seedling survival of two co-occurring oak species in southern California. *Forest Ecology and Management* 255:3063–3074.
- , B. KUHN, AND F. W. DAVIS. 2006. Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology* 81:127–152.
- WHITE, K. L. 1966. Structure and composition of foothill woodland in central coastal California. *Ecology* 47:229–237.
- ZAVALETA, E. S., K. B. HULVEY, AND B. FULFROST. 2007. Regional patterns of recruitment success and failure in two endemic California oaks. *Diversity and Distributions* 13:735–745.